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The life history of a temperate zone dragonfly living at the edge of its range with comments on the colonization of high latitudes by Neotropical genera of Zygoptera (Odonata)

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Abstract

Of the many Zygopteran genera that occur in the Neotropics, only five (*Hetaerina*, *Archilestes*, *Lestes*, *Argia*, and *Ischnura*) are represented north of 40°N in North America, and only three of these (*Hetaerina*, *Archilestes*, and *Argia*) probably had a tropical origin. In the two genera of Lestidae (*Archilestes* and *Lestes*) the life history of temperate-zone populations is usually regulated by an egg diapause, whereas in the two genera of Coenagrionidae (*Argia* and *Ischnura*) larval diapause synchronizes life histories with seasonal temperature changes. This paper presents data on the life history of a northern population of a species in the first genus, *Hetaerina americana* living in a geothermally influenced stream near to the northern edge of the species' range in western North America. Larval growth is affected by temperature and differs between warmer and cooler years, but generally larvae appear to grow very rapidly during summer and even grow over winter. Two peaks of larval recruitment each year and a decrease in final stadium size over the summer may be evidence for bi-voltinism, and the absence of final stadium larvae in October, November, and December indicates a short-day regulatory diapause in F-1 larvae. A long-day diapause which prevents autumnal metamorphosis of larvae appears not to be present. It is not known whether the tactics that allow New World species of Zygoptera to survive at mid- to high-temperate latitudes are also present in their tropical congeneric relatives, but it does appear that diapause expression has been associated with speciation in the temperate zone.

Introduction

The order Odonata is of tropical origin and although many species now live in temperate regions, they generally retain tropical traits such as an intolerance of low temperature (Pritchard 1982; Pritchard et al. 1996, 2000; Corbet 1999: 179ff.). However, of the genera of Zygoptera that occur in both tropical and temperate zones of the Americas, few occur north of Mexico and even fewer live at latitudes north of 40° in western North America. In fact there are only five of the latter – *Hetaerina*, *Archilestes*, *Lestes*, *Argia*, and *Ischnura* – representing only three families and leaving the majority of New World zygopteran families restricted to low latitudes (Paulson 2006).

Two of these genera are lestids. *Archilestes* has only two species in North America: *A. californicus* McLachlan occurs through all of the western coastal US States and has recently been recorded from the northern parts of the Mexican states of Sonora and Chihuahua (D. Paulson pers. comm.), but does not occur in Canada. The life history of northern populations is regulated by an over-wintering egg diapause (Kennedy 1915). *A. grandis* (Rambur) has a more tropical distribution. It has not been recorded north of ca 40°N but has been collected through Central America to Colombia. In the southern USA, populations may over-winter as larvae (Bick & Bick 1970).

The origin of the genus *Lestes* is unknown; the genus is cosmopolitan, occurring on all continents except Antarctica (Silsby 2001). Although represented in tropical America, there are twice as many species recorded from North America and more than twice as many in temperate zone South America as there are in the tropical Americas. The distributions of all but one of the six western North American species go no further south than the US, but some have been recorded north of the Arctic Circle in Canada. All of the North American species have univoltine life cycles. Most live in temporary ponds and survive the temperate zone winter in egg diapause, the anticipated habit of the last common ancestor of the North American *Lestes* (Stoks & McPeek 2006), but three species are restricted to permanent waters and have directly hatching eggs (Stoks & McPeek 2006).

How lestid life cycles are regulated in the tropics is unknown. All lestids listed in Corbet et al. (2006), including two tropical species, are said to be univoltine, and it is tempting to suggest that an obligatory egg diapause might be used to survive the tropical dry season. Indeed, F. Suhling (pers. comm.) reports that all *Lestes* known from Namibia are highly seasonal in reproduction, i.e. during the one rainy season, and that a univoltine life cycle is achieved by an egg and probably by an additional adult diapause. In Costa Rica, *Lestes tenuatus* Rambur and *L. forficula* Rambur appear to lay eggs at the beginning of the wet season, having spent most of the dry season as immature adults (D. Paulson pers. comm.) Similarly, in Gambia, Gambles (1976) reported that almost all *Lestes* species breed in temporary ponds in the rainy season, complete the larval stage in about two months, and spend the long dry season as adults in reproductive diapause. However, *Lestes plagiatus* Burmeister, which usually bred in permanent streams, emerged throughout the year and at no time was the population at any single stage of development. This may imply multi-voltinism in this species.

Another two of the five genera are coenagrionids. *Ischnura*, like *Lestes*, is cosmopolitan and there are more species known from North America than from tropical America and also, like *Lestes*, most western North American species do not occur south of Mexico. The only two that do occur south of Mexico occur no further north than the USA Border States with Mexico. *Ischnura* does not occur as far north as *Lestes*, although a relic population of *I. damula* Calvert occurs in hot springs at almost 60°N in British Columbia, Canada (Cannings 2002), and this species has been discovered in the last 10 years in Alberta, Canada, first around power plants but then in habitats with natural temperatures (Acorn 2004), suggesting recent immigration. Johnson (1964) found the majority of *I. damula* in New Mexico populations to be bivoltine. He believed that low winter temperatures retarded larval growth and prevented entry to the final stadium, finding a photoperiod effect to be inconclusive. It would be very interesting to know what happens in the Canadian populations, although clearly they have to be regulated.

The other coenagrionid genus is *Argia*, the most speciose genus of Odonata in the Neotropics. Although more than 30 species have been recorded from North America, many are restricted to Mexico and the USA Border States and most have limited latitudinal ranges. The two most northerly species in the west have rather different habitat requirements. *A. emma* Kennedy, which is not recorded from New Mexico, Arizona, southern California, or anywhere further south, occurs to the north in rivers, streams, and wave-washed lake margins up to southern British Columbia (Cannings 2002). *A. vivida* (Hagen) ranges somewhat further south – into Baja California – but has not so far been recorded from mainland Mexico. *A. vivida* is associated with stream outflows from springs and, particularly in the northern part of its range, with hot springs, as are some other *Argia* species (Pritchard 1991).

All of the coenagrionid species studied in the tropics and listed by Corbet et al. (2006) are recorded as having bivoltine or multivoltine life cycles. As latitude increases so the mode moves to longer life cycles, a major shift occurring above 40°N with a change to predominantly univoltine life cycles. Univoltine life cycles imply, but do not necessarily mean, that some sort of regulation is present and the temperate zone coenagrionids that have been well studied have life cycles that are regulated by photoperiod-cued larval diapause. The length of the life cycle of *Argia vivida* in the northern part of the species' range varies with temperature regime (Pritchard 1989) and a long-day diapause in late stadia occurs irrespective of whether the life cycle is one, two, or three years, while a short-day diapause in middle stadia occurs in two- and three-year life cycles, in accordance with Norling's (1984) seasonal regulation model. We know little about life history regulation in tropical coenagrionids, but given the lack of temperature and photoperiod variation which could govern larval diapause in tropical streams, we might expect that they may not be regulated. Of the seven species of *Argia* from Mexico for which Novelo-Gutiérrez (1992) gave flight information, adults of all but one were observed year-round, an indication that the life history is not regulated.

The last of the five genera is the calopterygid genus *Hetaerina*. Dumont et al. (2005) proposed that the Hetaerininae (their Hetaerinidae) radiated in the Neotropics, whereas the Calopteryginae (their Calopterygidae) radiated in the Palaearctic and Oriental regions, later entering North America via Beringia. In the Americas, the genus *Calopteryx* is limited to northern regions where it must live in cooler waters and presumably has larval diapause as European species do (Corbet 1957), whereas *Hetaerina* is still primarily Neotropical, with a species distribution similar to that of *Argia*. Although the year-round presence of adults indicates only that there is no regulation of the life history, it may be an indication of multi-voltinism, and on this basis several species of Central American *Hetaerina* are presumed to be multivoltine. Larvae of *H. capitalis* Selys and *H. cruentata* (Rambur) are in a range of sizes and adults are present throughout the year in Costa Rica (GP pers. obs.), and *H. titia* (Drury) and *H. americana* (Fabricius)adults occur year-round in Guatemala (Williamson 1923), as do adult *H. titia* in Florida (Davis & Fluno 1938). *H. americana* is multivoltine in Mexico (A. Cordoba-Aguilar pers. comm.). However, D. Paulson (pers. comm.) observed that there were essentially no *H. caja* Drury emerging during the fairly long dry season in Costa Rica, and he speculates that there could be some sort of dry-season diapause. At ca 21°S in Brazil De Marco & Cardoso Peixoto (2004) report that adults of *H. rosea* are present throughout the year, but with a single distinct peak in abundance during the rainy season from about September to June.

In the present paper I present data collected on the life history of *H. americana* living near to the genus' northern limit and compare this with the strategies of other mid-temperate zone Zygoptera which also occur in tropical latitudes, especially with *Argia vivida* which, like *Hetaerina*, belongs to a genus that almost certainly evolved in the tropics (Kalkman et al. 2008).

Study species

The genus *Hetaerina* is primarily Neotropical. Garrison (1990) recognized 37 species, with 13 species recorded from Central America (southern half of Mexico to Panama), 19 from northern South America (Colombia, Venezuela, Guyana, Surinam, French Guiana), and 26 from central South America (Ecuador, Peru, Bolivia, Paraguay, Brazil), although there are undoubtedly more species not yet described from South America. In contrast only three species are known from southern South America (Chile, Uruguay, and Argentina) and only four from North America (northern half of Mexico, USA, Canada). Thus the distribution of the genus is similar to that of *Argia* (Pritchard 1982), except that North America has no unique *Hetaerina*, whereas at least 15 species of the more speciose genus *Argia* do not occur south of central Mexico (data in Westfall & May 1996). Also, although both genera live in geothermally-influenced streams in the northern parts of their ranges, *Hetaerina* does not occur quite as far north or as far west as *Argia*. The most northerly species is *H. americana*, the subject of this paper. In western North America, *H. americana* is recorded from warm springs in northern Montana (ca 49°N) (Miller & Gustafson 1996), and a large population occurs in the Fall River and its geothermal tributaries around the town of Hot Springs, South Dakota (43°N), whereas *Argia vivida* reaches 51°N in warm springs in western Canada (Pritchard 1989). *H. americana* is not recorded from western Canada or Washington, Idaho or eastern Oregon (i.e. in the northern Cordillera) (Johnson 1973; Westfall & May 1996; Paulson 2005), regions where *A. vivida* (and warm springs) are common. Interestingly, at the time of Johnson's (1973) review of *Hetaerina* distribution, *H. americana* was not recorded from northern California or Oregon either, and records for Montana were dubious. Whether the recently established records for northern California, western Oregon, and a band from north to south through central Montana (Paulson 2005) reflect increased collecting or increase in temperature is not known. At the southern end of its range *H. americana* extends further south than *A. vivida* – into Nicaragua, whereas *A. vivida* has not been recorded south of the United States, except for Baja California. Johnson (1973) noted that the flight season of *H. americana* progressively shortens from seven months in the southern United States to about three months of the year in the most northerly populations, with low temperature probably playing the major role in limiting northward distribution. At a site in California at 39°N adults emerged continuously from April through November with peaks in June and August (Grether 1996). In Michigan there are also two peaks of adult abundance, one in mid- to late-July and the other a month later, in a flight season than runs from mid-June to late-September (Weichsel 1987).

Table 1. Mean daily air temperatures at Hot Springs, South Dakota, and calculated water temperatures in Hot Brook for various time periods. **tMda**: Mean daily air temperature [°C], **tCalMdw**: Calculated mean daily water temperature [°C] ± 95% confidence interval

Time period	Site	tMda	tCalMdw
01 ix 1992 – 30 iv 1993	1	1.99	13.96 ± 0.50
01 ix 1993 – 30 iv 1994	1	2.60	14.20 ± 0.43
01 ix 1999 – 30 iv 2000	2	4.99	15.17 ± 0.32
01 v 1993 – 30 ix 1993	1	16.12	19.66 ± 0.27
01 v 1994 – 30 ix 1994	1	19.22	20.91 ± 0.26 [1]
01 v 2000 – 30 ix 2000	2	18.68	20.69 ± 0.34
01 ix 1993 – 30 xi 1993	1	6.53	16.76 ± 0.47
01 ix 1994 – 30 xi 1994	1	9.43	16.96 ± 0.60 [2]
01 ix 2000 – 30 xi 2000	2	7.64	16.24 ± 0.79
01 xii 1992 – 30 xi 1993	1	6.43	15.75 ± 0.45
01 xii 1993 – 30 xi 1994	1	9.08	16.82 ± 0.44 [3]
01 xii 1999 – 30 xi 2000	2	9.30	16.91 ± 0.41

[1] Actual mean daily water temperature = 21.39 ± 0.24
[2] Actual mean daily water temperature = 17.13 ± 0.52
[3] Actual mean daily water temperature = 16.83 ± 0.47

Study site and methods

A population of *Hetaerina americana* was studied in Hot Brook (43°27'N, 103°30'W) in the town of Hot Springs in south-western South Dakota. Hot Brook has several atypical species of Odonata for the region (Provonsha & McCafferty 1977), including an isolated eastern population of *Argia vivida*, and is near the northern limit of the range of *H. americana*. Hot Brook's spring is one of two suppliers of domestic water for the town of Hot Springs and has a constant temperature of 23.5°C at the source. Two sites along Hot Brook were sampled. At Site 1, 1.5 km downstream from the source, continuous temperature records were taken with a Telog™ 2103E temperature recorder from November 1993 to December 1994. Water temperature at the site varied from a summer maximum of 26°C to a winter minimum of 6°C, with a daily fluctuation of ca 6°C in summer and 4°C in winter. Mean daily water temperature in Hot Brook was strongly correlated with mean daily air temperature recorded at the Department of Veteran Affairs' weather station in the town (Fig. 1) and so water temperatures could be predicted from air temperature records for periods when water temperatures were not recorded. Linear and exponential regressions of water temperature at Site 1 on air temperature gave equally good fits:

$$Y = 13.15 + 0.4037X \quad (r^2 = 0.92;\ F = 4{,}601;\ \text{d.f.} = 394)$$
$$Y = 12.72 * X^{1.0266} \quad (r^2 = 0.92;\ F = 4{,}413;\ \text{d.f.} = 394)$$

where Y = mean daily water temperature (°C)
X = mean daily air temperature (°C).

Between 1 December 1993 and 30 November 1994, the thermal sum at Site 1 in Hot Brook was 6,142 day-degrees above 0°C, representing a mean daily water temperature of 16.8°C, compared with a mean daily air temperature of 9.1°C at the Veterans Affairs station. Mean daily water temperatures for Site 1, calculated from the exponential regression equation, for several important time periods are given in Table 1.

At Site 2, 3 km from the source, continuous temperature records were taken from 13 October 2002 to 24 June 2003. Mean daily water temperature at the site varied from a maximum of 25°C to a minimum of 7.5°C over this period, with a daily fluctuation of ca 6°C in summer and 4°C in winter. Again, mean daily water temperature at Site 2 is strongly correlated with mean daily air temperature recorded at the Department of Veteran Affairs' weather station in the town, with an exponential regression of water temperature on air temperature giving a somewhat better fit than the linear fit:

$$Y = 12.46 + 0.3545X\ (r^2 = 0.86;\ F = 1571;\ \text{d.f.} = 253)$$
$$Y = 12.22 * X^{1.0257}\ (r^2 = 0.89;\ F = 1981;\ \text{d.f.} = 253)$$

where Y = mean daily water temperature (°C)
X = mean daily air temperature (°C).

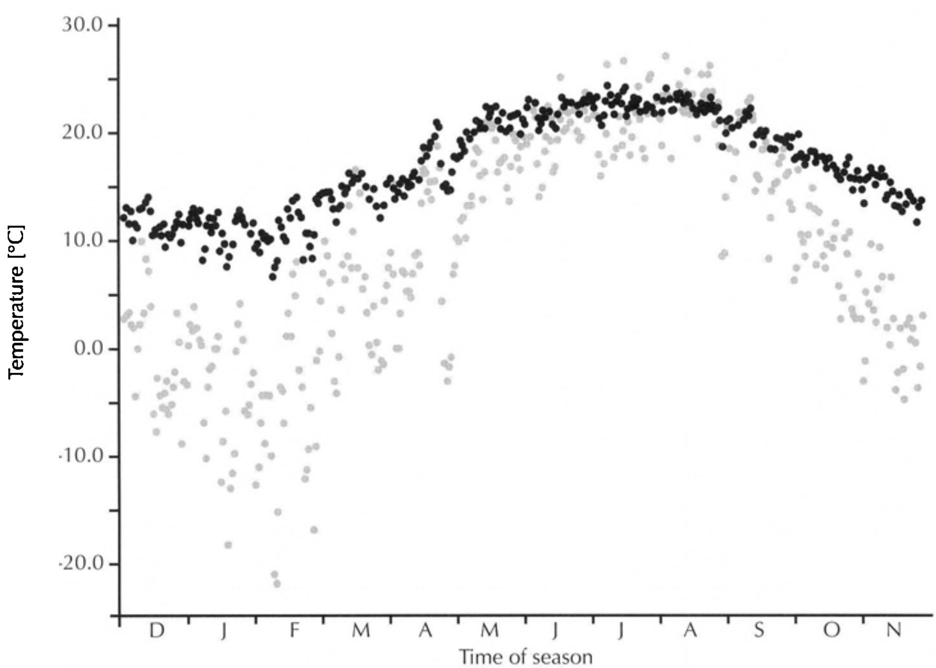

Figure 1: Mean daily water temperatures (●) from Site 1, Hot Brook, South Dakota and mean daily air temperatures (●) in the town of Hot Springs from December 1993 to November 1994.

The regression equations show that Site 1 was warmer than site 2 by ca 0.5°C at an air temperature of 0°C and by ca 1.5°C at an air temperature of 25°C, presumably because Site 1 is closer to the source. Mean daily water temperatures at Site 2, calculated from the exponential regression equation, for several important time periods are given in Table 1.

Larval samples were taken at 1- to 3-month intervals from Site 1 between October 1992 and December 1994, and from Site 2 between June 1999 and December 2000. Although sampling was not quantitative, ca 5 m of in-stream vegetation (mainly sedges) on each side of the stream was thoroughly swept with a double net on each occasion. Larvae collected in the inner 0.8 mm mesh net were sorted in white enamel trays at the site and preserved in 70% ethanol, while the contents (mainly detritus) of the outer 0.2 mm net were preserved in 10% formalin at the site and later sub-sampled and sorted under the microscope in the laboratory. Head capsule widths of *H. americana* larvae were measured to the nearest 0.04 mm under the microscope and plotted as frequency distributions for each sampling date using the KiteGraph™ programme developed by Karl Norling <http://home.swipnet.se/kitegraph/>. Frequency distributions were also plotted with size in units of 0.05 on a natural logarithmic scale from -1.2 (0.3 mm) to 1.55 (4.7 mm). The logarithmic scale more accurately represents the geometric growth pattern of larval insects and makes it somewhat easier to distinguish cohorts. The head width differences between the last few stadia were initially defined by groupings observed in plots of head width against meta-thoracic wing-pad length.

Results

Adult *Hetaerina americana* flew on sunny days from at least early May through September at Hot Brook; teneral adults have been seen on 3 May and mature adults on 1 October. Larval size-frequency diagrams from October 1992 to December 1994 at Site 1 are shown in Figure 2 and from June to December 2000 at Site 2 in Figure 3. The youngest larvae, probably between stadia F-12 and F-6 (head capsule width: 0.31 - 1.5 mm), were present in all samples from June through September, as well as the 8 December 2000 sample. F-1 larvae (head capsule width: 2.72 - 3.32 mm) were collected in every sample except for those from 1 October 1992, 25 September 1993, and 27 September 2000. Final stadium (F) larvae (head capsule width: > 3.32 mm) were present from February (1994) and March (1993) through the summer months, but were not collected in October, November, and December samples. The size of F larvae decreased during each summer (Table 2), but was the same in June in 1994, 1999, and 2000. F-1 and F-2 larvae were also smaller in summer compared with autumn, winter and spring samples.

A range of stadia was present in every month, and in samples from June through September at Site 1 this range was composed of two size cohorts (Fig. 2), while there may have been three size cohorts present at Site 2 in the summer of 2000 (Fig. 3). Only one cohort is apparent during the rest of the year at Site 1. Peaks of larval recruitment were evident in the data in September 1992, September 1993, and June-July 1994 at Site 1. The September recruitment cohorts disappeared during the winters of 1992/1993 and 1993/1994. Larval recruitment was more continuous in 2000 at Site 2 (Fig. 3), but was larger in June and September than in July and December, The size distribution in June 2000 suggests that two cohorts came through

Table 2. Mean head width [mm] 95% confidence interval of larval stadia of *Hetaerina americana* in Hot Brook. Data for 1993 and 1994 are from Site 1; data for 1999 and 2000 are from Site 2.

Date	F-2	*n*	F-1	*n*	F	*n*
20 iii 1993	2.274 ± 0.044	29	3.020 ± 0.048	27	3.908 ± 0.048	26
17 vi 1993	2.171 ± 0.040	25	2.914 ± 0.066	20	3.792 ± 0.037	42
25 ix 1993					3.598 ± 0.191	2
11 xi 1993			2.987 ± 0.062	23		
03 ii 1994			3.015 ± 0.062	66	3.802 ± 0.078	4
03 v 1994			2.788 ± 0.043	24	3.787 ± 0.037	32
16 vi 1994	2.176 ± 0.037	14	2.805 ± 0.037	20	3.725 ± 0.022	33
27 vii 1994	1.964 ± 0.023	42	2.602 ± 0.032	27	3.528 ± 0.036	46
06 x 1994			3.079 ± 0.082	7		
13 xii 1994			3.073 ± 0.037	20		
23 vi 1999	2.162 ± 0.050	12	2.866 ± 0.039	24	3.773 ± 0.028	56
05 vi 2000	2.198 ± 0.045	15	2.875 ± 0.034	33	3.762 ± 0.105	7
23 viii 2000			2.680 ± 0.022	53	3.551 ± 0.023	65
27 ix 2000					3.734	1

the winter of 1999/2000 at Site 2 and the September 2000 recruitment was still present in December 2000 (Fig. 3).

Figure 4 shows the early summer, autumn, and early winter data from 1993 and 1994 at Site 1 and from 2000 at Site 2 so that the population structure can be more easily compared between sites at these time periods and related to the water temperatures in Table 1. It is apparent that there were differences in population structure between years and sites.

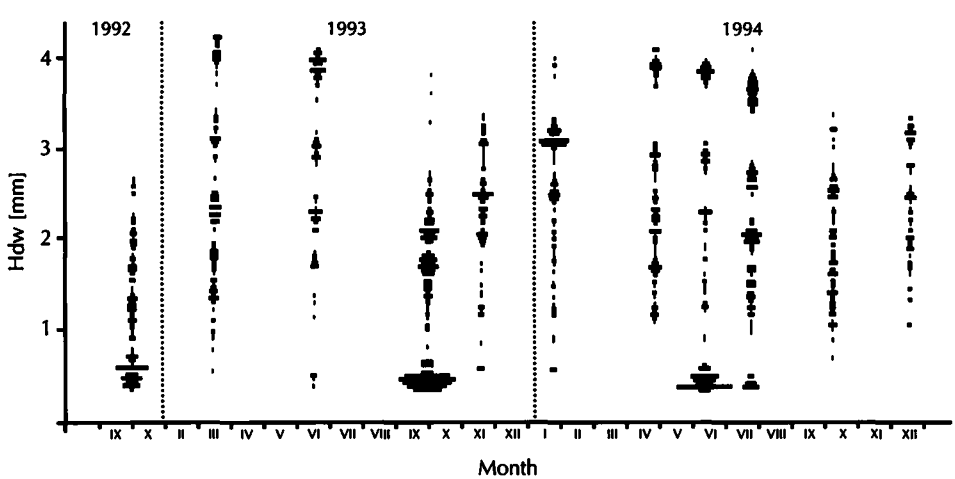

Figure 2: Larval size-frequency diagram for *Hetaerina americana* from October 1992 to December 1994 at Site 1, Hot Brook, South Dakota. Size is recorded as head width across the eyes in mm; ▬: 10 specimens.

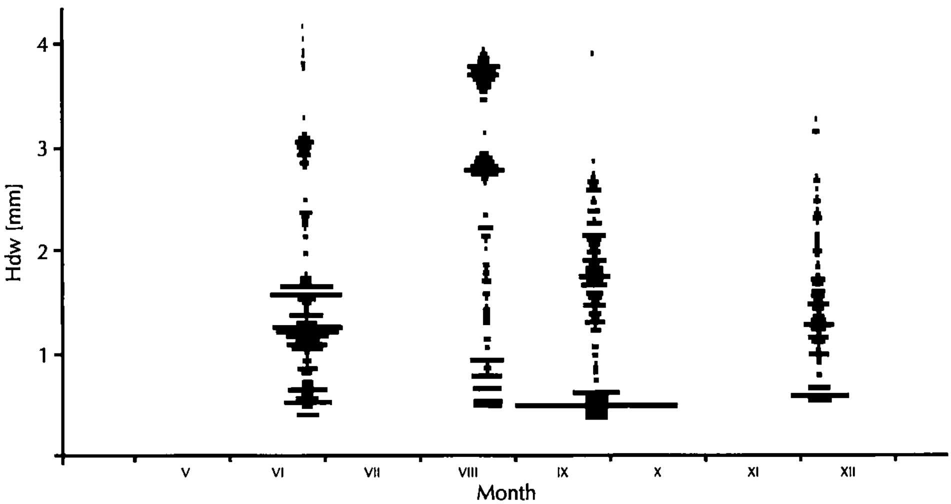

Figure 3: Larval size-frequency diagrams for *Hetaerina americana* from June to December 2000 at Site 2, Hot Brook, South Dakota. Size is recorded as head width across the eyes in mm; ▬: 10 specimens.

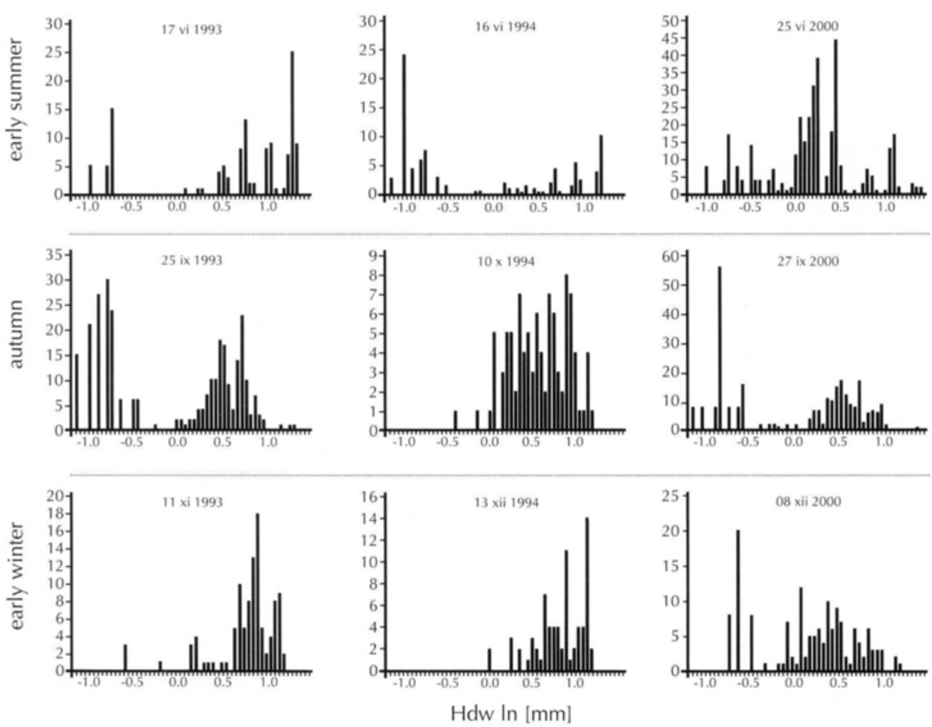

Figure 4: Larval size-frequency diagrams for *Hetaerina americana* from early summer, autumn, and early winter at Hot Brook, South Dakota. Data for 1993 and 1994 are from Site 1; data for 2000 are from Site 2. Size is recorded as ln of head width across the eyes in mm.

Discussion

The data collected in this study from Site 1 in 1993 and 1994 are not easy to interpret and raise a number of questions. For example a number of questions arise from the presence of distinct peaks of larval recruitment: Given that adults are present throughout the summer, why are there peaks of larval recruitment in June and September and why were both of these recruitment periods not evident in each year at Site 1? What happens to the larvae in these recruitment peaks, as very few larvae with head widths just below 1 mm appeared in the samples? Do they have very low survival or do they grow very rapidly to merge with the older cohort?

These questions may arise in part because of inadequate sampling of small larvae. The October 1994 sample has a similar cohort structure to the 1992 and 1993 autumn samples, but differs from the other years in lacking a distinct recruitment cohort. As no sample was taken in September 1994, it is possible that the recruitment cohort was missed, especially as the summer was particularly warm. And if there was no recruitment, the size distribution would indicate no larval growth over the summer. By October the recruitment cohort could have already merged with the older cohort, or become the older cohort if a bivoltine alternative (see below) for this summer is correct. There were already plenty of final stadium larvae in late July and adult emergence in July and August would have led to recruitment at least by September. Similarly, final stadium larvae in March and June 1993 must have emerged and given rise to an early summer recruitment cohort, of which the few early stadium larvae in June 1993 were presumably a part. And if there was no recruitment peak in early summer 1993, the group of larvae near 2 mm in September is unexplained. Had samples been taken in May, July, and August 1993, and in August and September 1994, the recruitment picture may have been more like the situation in 2000 when recruitment was more continuous, but still with peaks in June and September (Fig. 3).

The data indicate that considerable growth of larvae of *Hetaerina americana* in Hot Brook takes place even during winter when water temperature is 10-15°C and that larvae grow very rapidly during summer. The two peaks of larval recruitment (see also the two emergence peaks of Weichsel 1987; Grether 1996) indicate bi-voltinism as does the decrease in size of F, F-1, and F-2 stadium larvae over the summer as a result of very fast growth (Norling 1984; Johansson & Norling 1994). My observations on *H. capitalis* and *H. cruentata* in Costa Rica at a similar temperature suggest that *Hetaerina* larvae are capable of rapid growth, and other Zygopterans can complete a generation in similar or shorter periods of time at similar temperatures to those in the summer in Hot Brook (Corbet 1999: 630). Hot Brook accumulates ca 2,500 day-degrees above 10°C during the year, and if *H. americana* has a similar relationship between growth rate and temperature as *Argia vivida* (Pritchard 1989), it should be univoltine in Hot Brook. However, we know nothing about the relationship between temperature and growth rate in *Hetaerina*, although observations in Costa Rica where *H. capitalis* appears to be multivoltine at a constant temperature of 20°C suggest that species of *Hetaerina* are capable of much faster growth than *Argia*. *Hetaerina* larvae are built much more like lestids than coenagrionids such as *Argia* and if they have similar behaviour to *Lestes* we might expect their growth rates to be high compared with other Zygoptera (Pickup & Thompson 1990; Krishnaraj & Pritchard 1995; Pritchard et al. 2000). *Hetaerina* larvae do not perfectly fit the model

Table 3. Mean head width [mm] 95% confidence interval of larval size cohorts of *Hetaerina americana* at Hot Brook. Data for 1992 and 1994 are from Site 1; data for 2000 are from Site 2. *n*: number of individuals in sample; %: percentage of sample represented by each cohort.

Date	*n*	Cohort 1	%	Cohort 2	%	Cohort 3	%
01 x 1992	152	0.486 ± 0.026	43	1.547 ± 0.094	57		
20 iii 1993	134			2.445 ± 0.160	100		
17 vi 1993	126	0.436 ± 0.044	20	2.890 ± 0.167	80		
25 ix 1993	298	0.424 ± 0.014	46	1.782 ± 0.057	53	3.462 ± 0.519	1
11 xi 1993	105	1.089 ± 0.167	14	2.430 ± 0.081	86		
03 ii 1994	133	1.135 ± 0.154	14	2.723 ± 0.084	86		
03 v 1994	140	1.455 ± 0.074	29	2.816 ± 0.140	71		
16 vi 1994	184	0.397 ± 0.014	55	2.757 ± 0.284	45		
27 vii 1994	184	0.382 ± 0.020	10	2.346 ± 0.132	90		
06 x 1994	105			1.885 ± 0.116	100		
13 xii 1994	72			2.331 ± 0.138	100		
25 vi 2000	329	0.549 ± 0.028	23	1.266 ± 0.030	60	2.776 ± 0.129	17
23 viii 2000	212	0.731 ± 0.064	33	1.855 ± 0.108	12	3.165 ± 0.080	55
27 ix 2000	277	0.454 ± 0.017	43	1.753 ± 0.068	57		
08 xii 2000	158	0.519 ± 0.016	23	1.499 ± 0.090	77		

of fast life style as *Lestes* larvae do (Johansson 2000) in that they do not live in ephemeral habitats and are not characterised as highly active larvae. However, they are likely vulnerable to fish predation in Hot Brook and probably do have quite restricted microhabitat requirements, both characteristics associated with a fast life style (Johansson 2000). Also, the abundance of food in Hot Brook should support a fast growth rate. Furthermore, there are no observations on behaviour of *Hetaerina* larvae (Cordoba-Aguilar & Cordero-Rivera 2005), either in their natural habitat or in the laboratory; in fact their sluggish characterisation seems to be built solely on a supposed similarity to *Calopteryx* (e.g. Walker 1958; Westfall & May 1996), perhaps an inappropriate comparison given that *Calopteryx* probably evolved and still lives in relatively cold northern waters (Dumont et al. 2005) whereas *Hetaerina* evolved in warm tropical habitats.

Further evidence for rapid growth in *H. americana* is suggested by the samples from 25 September 1993, with a large recruitment cohort, and from 11 November 1993. Although the number of young larvae is reduced from 46% of the population in September to 14% in November (a level that is maintained in February), the cohort is still distinguishable and larvae have apparently grown in mean head width from 0.42 mm to 1.1 mm over a 47 day period during which only 294 day-degrees above 10°C were accumulated.

Also there is evidence for faster growth in warmer years. For example, the 1994 summer was significantly warmer than the summer of 1993 (Table 1) and although the pattern in early May 1994 at Site 1 is similar to that in March 1993, the sizes of all putative stadia are smaller in 1994 (Fig. 2; Table 2). Then the sample in June 1994 differs from that in June 1993 in that there is a larger recruitment cohort, perhaps because the warmer year has produced an earlier emergence of adults. In the

July 1994 sample, 41 days later, the proportion in the recruitment cohort is much reduced (Table 3) and the mean larval size in the older cohort has dropped due to the addition of larvae at the lower end of the size range. Thus, the older larvae in the June recruitment cohort have apparently already merged with the older cohort. Alternatively, the older cohort in July may represent the whole of the June recruitment and it is possible that the whole of the population was bivoltine. To complete a generation over the summer of 1994, the smallest larvae must have grown from ca 0.4 mm to 1.5 mm head width and the largest larvae from 0.55 mm to 3.5 mm in 41 days at a mean water temperature of 22°C and with a temperature accumulation of 492 day-degrees above 10°C.

The size-distribution pattern in June 2000 at Site 2 differs from that in June of other years at Site 1 in that there appear to be three cohorts present (Fig. 4). The first is the early summer recruitment cohort. The second is not represented in Site 1 samples, but perhaps represents the previous year's late summer recruitment. The third is the same mean larval size as the older June cohort in other years, but the mode is in the F-1, not in the F stadium. In August 2000, the second cohort has disappeared, and more than half of the sample is in the F and F-1 stadia. However, these F-1 and F larvae are smaller than in the June sample, again indicating fast growth over the summer. Only two cohorts are present in September 2000, the largest limited at the F-2 stadium, and very similar to the situation in September 1993 at Site 1 (Fig. 4). Presumably the recruitment cohort has been produced by adults developing from the August F and F-1 larvae. In December, there are again two cohorts; some of the larger larvae are now in F-1, but the oldest group has a smaller mean larval size than in September, presumably a result of augmentation from the recruitment cohort. The fact that the recruitment cohort is clearly present in December may reflect a warmer winter (Table 1), leading to a longer adult flight period and perhaps better early larval survival. The calculated water temperature in autumn and winter of 1999-2000 at Site 2 was significantly warmer ($p < 0.05$) by a degree or more per day than the two years I sampled at Site 1 (Table 1).

The absence of final stadium larvae in October, November, and December samples may indicate a short-day regulatory diapause in F-1 larvae, similar to that of *Argia vivida* at similar latitudes. Temperatures in October are still reasonably high, certainly higher than in February and March when F stadium larvae *are* present, and if no diapause was present in pre-final stadia we would expect final stadium larvae to be present in the autumn. However, the long-day diapause which prevents autumnal metamorphosis of larvae (Norling 1984), and which is present in *A. vivida* (Pritchard 1989), appears not to be present in *H. americana* and may allow it to be bivoltine. Thus, the life history of *H. americana* in South Dakota appears to fit the "lower temperate latitudes" model of Norling (1984) rather than the "higher temperate latitudes" model (Norling 1984; see also Ingram & Jenner 1976 for *Enallagma aspersum* [Hagen] in North Carolina). However, while not wanting to rule out at least partial bi-voltinism, the simplest categorization of *H. americana*'s life history in Hot Brook is that of a one-year life cycle, with a great deal of individual variation in growth rate from place to place and year to year as a result of variation in temperature. The large size of final stadium larvae (and presumably adults) early in the year could then be correlated with the short-day diapause in the previous autumn, while the small size of late-summer soon-to-be emergents might be the result of forced development in larvae that have over-wintered as small larvae (U. Norling pers. comm.).

A final conclusion is that the tactics that allow New World species of tropical genera to survive at mid- to high-temperate latitudes – egg diapause in *Archilestes californicus* and larval diapause in *H. americana* and *Argia vivida* – are not only similar in their con-familial temperate-zone relatives (e.g. *Lestes* and *Ischnura*) but apparently are not expressed in their tropical congeneric relatives; they appear to be associated with speciation in the temperate zone. Tauber & Tauber (1981) argued that tropical populations of species that extend from tropical to temperate zones generally have the capability to enter diapause, even though they may not express it every year because they rely on subtle changes in environmental factors that vary from place to place and year to year. Reviews by Tauber et al. (1986) and by Danks (1987) make the points that diapause is a relatively simple adaptation to develop; differences in diapause expression in some species are under relatively simple genetic control; and selection for diapause in allopatric populations may reinforce speciation and give rise to the current distribution of species. In Zygoptera there is generally a sharp disjunction between temperate and tropical species giving support to this view of diapause expression.

Another useful approach might be to turn the question around and ask not how *Hetaerina* and *Archilestes* and *Argia* have been able to expand their ranges northward, but to ask why other Neotropical Zygoptera have *not* been able to expand their ranges into temperate latitudes. Part of the reason for the restriction of *Cora marina* Selys to low latitudes is undoubtedly its adaptation to seasonally torrential streams (Pritchard 1996). *C. marina* has a univoltine life cycle in Costa Rican streams, due in part to spending the early part of its larval life in the hyporheos where food and feeding opportunities are limited (could this be a form of diapause induced by food limitation?), and to a requirement for water-soaked logs above the stream for oviposition. Presumably, *Hetaerina*'s habitat in the same streams in Costa Rica – exposed fine tree roots in the water pools at the edges of the streams – places no limitation on their feeding opportunities and probably allows them to be multivoltine, although differences in growth rate may also be involved.

Clearly there are currently more questions than answers to the colonization of temperate latitudes by tropical Zygoptera. Answers to these questions will not be readily forthcoming until we know much more about the life histories of more populations in the tropics and of populations in the transitional zone at the northern limit of tropical species and the southern limit of temperate zone species.

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